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Observations on the Shell structure of Calyptogena

(Vesicomyidae; Bivalvia; Mollusca)

by

Jean-Jacques OBERLING
Musée d'Histoire Naturelle
Bern, Switzerland

and

Kenneth Jay BOSS
Museum of Comparative Zoology
Harvard University
Cambridge, Mass., U.S.A.

With 2 fig. and 1 plate

INTRODUCTION

Recently a number of new species of the predominantly archibenthic bivalve family Vesicomyidae have been described (Boss, 1967; 1968). Representatives of this group are distributed throughout the world and have been encountered by nearly every deep-sea expedition; their position in relation to other heterodont bivalves has been contested (Boss, in press).

Calyptogena was introduced by Dall (1891) into the family Carditidae and subsequently considered in the Arcticidae (Cyprinidae) by Okutani (1966). With all vesicomyids, *Calyptogena* shares the common features of a dehiscent periostracum, posteriorly sinuous pallial line, chalky shell and more or less deep-sea habitat. The unusually thick, ponderous shell and the peculiar dental and ligamental characteristics of *Calyptogena* are distinctive (Boss, 1968). The microscopic structural features of the shell were deemed promising characters to determine the systematic placement of *Calyptogena* and its allies.

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METHODS AND SECTIONS

The sections have been studied in ordinary and polarized light with magnifications of up to 700. Sections of various orientations were observed, but the most useful were found to be the vertical radial sections. The grained structure of the ectostracum of *C. ponderosa* appears much the same in sections of all orientations, and the inner layers are virtually homogeneous in horizontal sections. Polished and thin sections were prepared by cutting and grinding with a diamond wheel and fine carborundum abrasive.

DESCRIPTION

The genus **Calyptogena**

Calyptogena Dall 1891, Proc. U.S. Nat. Mus., 14:189 (type-species, by monotypy, *Calyptogena pacifica* Dall, 1891, p. 190; type-locality, *Albatross I* station 3077, off Dixon Entrance, Alaska in 322 fathoms).

Six species are known in the genus *Calyptogena*, and four of these are concentrated in the Caribbean-Eastern Pacific area. The west African, *C. valdiviae* and the Japanese, *C. soyae* are the remaining species. *C. stearnsii* and *C. lepta* of the eastern Pacific are tentatively placed in the genus while *C. pacifica*, the type-species also from the eastern Pacific, and *C. ponderosa* from the Caribbean Sea are among the most distinctive forms. All species are archibenthic, living in comparatively deep water usually in soft, muddy substrates; *C. valdiviae* has been taken in 2500 meters. Only the shell microstructure of *C. pacifica* and *C. ponderosa* was studied.

Macroscopic characters of the shell

Maximum length 114 mm, maximum height 76 mm, weight to 140 grams, elongate-elliptical to subovate in outline, inequilateral, equivalve, heavy and solid. Sculpture irregular, not well developed, consisting of fine concentric lirations;

growth rings sometime evident. Escutheon usually deeply excavated; ligament posterior, strong, deeply inset, and subtended by raised nymphal callosities. Right valve with two cardinal teeth beneath umbo; dorsal tooth broad and thickened; ventral tooth narrow. Left valve with two subumbonal cardinal teeth; posterior tooth larger and rather pointed; anterior tooth smaller and rather thickened; additional posterior cardinal tooth consisting of elongate crease beneath nymphal callosity. Adductor muscle scars subequal; pallial line weakly sinuous posteriorly. Shell substance chalky; covered in living specimens with dehiscent periostracum.

Microscopic characters of the shells [1]

The shell of *Calyptogena ponderosa* has a grained ectostracum and a very vaguely structured, almost homogeneous mesendostracum. The same structure is found in the other *Calyptogena* examined here, *C. pacifica*, though there are differences in the relative thicknesses of the outer two layers and in other details which will be mentioned later. It is, incidentally, the grained and rather loose structure of the ectostracum which produces the chalky appearance of the shell surface of *Calyptogena*.

Ectostracum

The ectostracum of *Calyptogena ponderosa* (Pl. I, figs. 1, 2), secreted on the rather deep, non-reflected marginal region of the shell, attains a thickness of about 1½ mm in the adult, which is unusually thick when considered in relation to the shell as a whole, whose maximum thickness, outside the hinge, is little more than 2 mm. The structure of this ectostracum is that referred to as grained by Bøggild (1930, pp. 250 and 286). This, in the upper portions of the layer, is as indicated on fig. 1 and Pl. I, fig. 1. The bigger grains average about 5 microns in diameter and grade down to granules of ½ micron or even less (fig. 1). These grains are irregular in shape, generally with angulations, and sometimes even embayments (fig. 1). The grains, in this portion of the layer, tend to be at least partially isolated from each other by well defined walls that show up clearly even in non-polarized light. These walls together form a very complex pattern, labyrinthic where cell walls are not complete or cellular where they are, and speckled with various inclusions. The portions of grain boundaries that are not set out by walls may be determined through the different aspect of the individual grains under polarized light, the extinction pattern being generally distinct for each grain. Small walled granules may appear here and there between the grains, but granules are especially common within these main structures, to the extent that the latter often seem to be virtually composed of aggregates of the former. Such " internal " granules are not separated

[1] The layer terminology used here is that introduced by Oberling (1955).

by walls but are distinguished as brighter areas within the grains. Reflected light beams and differential refraction from the irregular grain surfaces might account for part of this phenomenon, but since luminous granules also show up in otherwise relatively homogeneous areas, where grains are absent, it appears unlikely that all such granules are mere optical phenomena.

Further down in the layer there appears a gradually clearer differentiation between grains that are bounded by walls and those that are not, the former

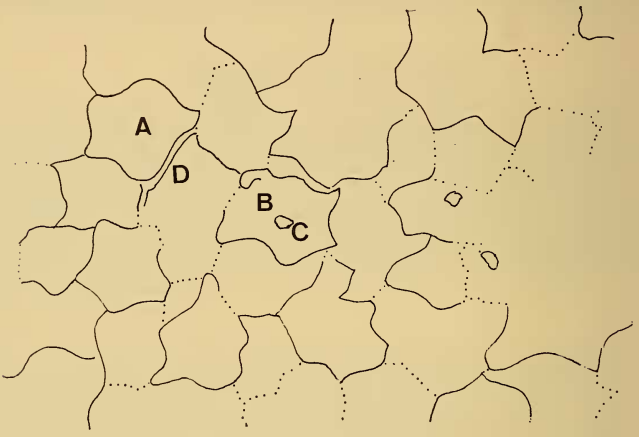

FIG. 1.

Grained structure of ectostracum of *C. ponderosa*
A. Normal big grain, with a 5mμ diameter
B. Irregular, embayed grain.
C. Granule within (or below, or above) grain.
D. Grain non-contiguous with its neighbour.
Solid lines = " walls "
Dotted lines = limits of grains as determined by differential refraction.

becoming very strongly defined, the others tending more and more to form an almost homogeneous " ground " whose components become distinct only at about extinction [1]. The well defined grains tend to become scarcer further down in the ectostracum until close to the base of that layer, they are usually few and far apart.

Near the base of the layer, all major units tend to show an increase in size, and grains there are 20 or more microns in diameter. Just above the mesectostracal boundary is generally found a thin sublayer of well bounded grains that are often

[1] The optic axes are, so far as this « ground » is concerned, on the whole perpendicular to the growth lines, as is the case for the lower layers, but extinction is more complete for some grains of this « ground » than for others, and it is thus that they may still be differentiated.

elongate in the vertical direction and that may even show an overlapping pattern with the lower grains appearing to overlap on those above [1].

A few growth sublayers (OBERLING, 1964) in the adult part of the shell also show coarse and elongate grains, and these tend often to exhibit, as they do in the lowermost ectostracum, a radial extinction, as in the case of complex structures (BØGGILD, 1930, p. 255).

In addition to all the preceding, opaque granules, probably similar to the " granula " mentioned by NEUMANN (1959) for the gastropod *Theodoxus*, appear on thick sections of *Calyptogena*. These may reach a diameter of 2 microns or even more, appear to be of a very complex nature and contribute greatly to the general opacity of the ectostracum. They are somewhat patchy in distribution, and within each of these areas are often aligned along growth lines.

The ectostracum of *Calyptogena pacifica* (Pl. I, fig. 3) is structurally very similar to that of *C. ponderosa* in its upper portions, but differs from the latter in that it maintains this same structure throughout its thickness.

Mesostracum

This layer is extremely thin in *Calyptogena ponderosa* (only about 1/30 of the ectostracal thickness) and appears as a shiny film on the inside of the shell between the pallial line and the margin. Its structure would have been considered homogeneous by BØGGILD (1930, p. 245). Indeed, little trace of any structural element is observable in ordinary or polarized light, except at or near extinction. Under such conditions, vague outlines of major, more or less vertically oriented elements of uncertain identity may be discerned, as well as a more or less right angled network of irregular, mostly lamellar, platelets that show little evidence of relationship to these outlines but may nevertheless represent some kind of incipient or residual second-order lamellation (fig. 2).

No opaque " granula " could be discerned in the mesostracum of the main portion of the shell, which fact explains its lesser opacity as compared with the otherwise identically structured endostracum. The optic axes are vertical throughout, (*i.e.* perpendicular to the growth planes) and the extinction is much more complete than in the case of the endostracum beneath.

In the hinge the mesostracum is much thicker and moreover shows a slightly different structure than in the main shell portion. In the young stages of that region of the shell, the structure of the layer is grained, much as in the ectostracum with, moreover, an extreme profusion of opaque " granula "; later on, the structure becomes much more like that in the rest of the mesostracum, except that here the " major structures " are more clearly defined, and in part at least of the complex-crossed-lamellar type (see BØGGILD, 1930, p. 255).

[1] Although of course it is those above that are secreted between the ends of those below.

The mesostracum of *Calyptogena pacifica* has the same structure as that of *C. ponderosa*. However, it is relatively and absolutely much thicker (about 4 times as thick as the ectostracum, but getting much thinner towards the apex). Further, its structure in the hinge is much more similar to that in the main body of the valve than is the case for *C. ponderosa*.

Endostracum

The structure of the endostracum is much like that of the mesostracum, and in fact some of the vaguely outlined major structural elements are, to all evidence continuous from one layer to the next. The platelets are not everywhere present, and especially where the outlines of the main structures are relatively well defined, may be obsolescent or lacking altogether.

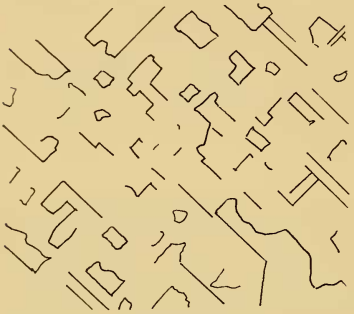

FIG. 2.

" Platelets " of the lower two layers of *C. ponderosa*. Main structures about 5 μ across.

Some portions of the upper part of the layer show quantities of light spots of grain or granular size (Pl. I, fig. 2, 6, light upper regions); a few very thin sublayers of prisms and granules may be observed, and opaque granula similar to, though of somewhat smaller size than those of the ectostracum show up, especially in the upper portions of the layer; the optic axes are, as in the mesostracum, perpendicular to the growth planes, but the extinction tends to be here much less complete.

The endostracum of *C. pacifica* is very similar to that of *C. ponderosa*, but no sublayers of prisms or granules could be detected.

Periostracum, Myostracum

Both these layers are present and both very thin, the pallial myostracum often appearing as isolated prisms, separated from each other by wide areas where that layer is totally absent, and hence the mesostracum and endostracum in direct contact.

DISCUSSION

DALL (1891) originally placed *Calyptogena* in the Carditidae; his decision may have been based on the superficial resemblance of the hinge structure of *Calyptogena pacifica* and *Cardita affinis* Sowerby from the west coast of Mexico.

Certainly the configuration of the cardinal teeth in both these species is similar, but upon closer examination it appears to be of a superficial nature. *Cardita* has a distinctly bilobed and protuberant subumbonal cardinal tooth, whereas in *Calyptogena* the heavy subumbonal cardinal is merely blunt, not bifid, and anteriorly coextensive with the anterior cardinal tooth which parallels the hinge line. Distal lateral dental elements are evident in *Cardita* but lacking in *Calyptogena*.

Macroscopic characteristics which indicate that *Calyptogena* is not of carditid affinities include the general structure of the shell. Carditid traits such as strong radial sculpture, ventral crenulations, polished interior, and brownish coloration are totally dissimilar to the chalky, ponderous, smooth, and whitish valves of *Calyptogena*. In addition, many carditids are byssate and live in shallow water; *Calyptogena* does not have a byssus—at least in the adult condition—and inhabits deep water.

Of all the shells known to the authors, those of *Arctica islandica* and that of the venerid *Tivela stultorum* most closely approximate the structure of *Calyptogena*.

The structure of *Arctica islandica* is very close to that of *Calyptogena*, with a grained ectostracum and mostly homogeneous mesendostracum; however, in *Arctica*, the mesostracum is grained in the younger growth stages of the shell, and the endostracum contains many sublayers of grains and granules, which produce the excellent parting planes that are a plague to those trying to section that mollusk. The opaque granula also are extremely numerous and in the endostracum tend to be elongate and come to resemble tubules.

In the earlier stages, *Tivela stultorum* of the Veneridae shows a structure very similar to that of *Calyptogena* (grained ectostracum, mesendostracum with a homogeneous, vaguely complex structure), while in the later growth stages crossed-lamellae appear that finally make up the whole ectostracum and upper mesostracum, as in many other venerids (Oberling 1964, p. 40).

Bøggild (1930, pp. 278-9) included *Cardita* in his discussion of the Astartidae. In this genus and related ones (*Beguina*, etc.) the shells are structurally rather uniform and possess a mesectostracum of crossed-lamellar structure and a complex endostracum, all structures being typically and fully developed. Moreover, there is a rather dense system of tubulation that runs through the two lower pallial layers and is very characteristic of the Carditidae (Oberling, 1964).

In contrast to *Cardita*, the shell of *Calyptogena* has, as indicated above, a homogeneous mesendostracum with traces of complex structure, while the ectostracum is grained throughout, or almost so. When these differences are added to the gross morphological differences between the Vesicomyidae and Carditidae, it appears evident that *Calyptogena* could not possibly be closely related to the Carditidae.

In view of the structural similarity of *Calyptogena* to certain venerids and to *Arctica islandica*, which has been considered veneroid in its affinities (Nicol, 1951),

it is most probable that this genus and the Vesicomyidae, as a whole, are closely allied to the Veneridae and should be at least considered in the superfamily Veneracea along with the Veneridae, Cooperellidae and Glauconomidae (NEWELL, 1965).

SUMMARY

The shell structure of the archibenthic pelecypods *Calyptogena ponderosa* and *C. pacifica* has been examined with the polarizing microscope. It was found that the outer calcareous layer was grained, the two inner layers more or less homogeneous. This structure is very close to that of *Arctica islandica* and of some Venerids such as *Tivela stultorum*, and it is thus probable that *Calyptogena* is related to these forms rather than to the genus *Cardita*, as had been proposed by Dall.

ZUSAMMENFASSUNG

Die Schalenstruktur der beiden Muscheln *Calyptogena ponderosa* und *C. pacifica* wurde mit Hilfe des Polarisationsmikroskopes untersucht. Es wurde festgestellt, dass die äussere Kalkschichte granuliert ist und die beiden inneren Schichten mehr oder weniger homogen sind. Diese Struktur steht derjenigen von *Arctica islandica* und von einigen Veneriden wie *Tivela stultorum* sehr nahe und es ist daher wahrscheinlich, dass *Calyptogena* mit diesen Formen mehr verwandt ist als mit der Gattung *Cardita*, wie Dall vorgeschlagen hatte.

RÉSUMÉ

La structure de la coquille des lamellibranches archibenthiques *Calyptogena ponderosa* et *C. pacifica* a été étudiée à l'aide du microscope polarisant. Il a pu être constaté que la couche calcaire extérieure est granuleuse; les deux couches intérieures sont plus ou moins homogènes. Cette structure est très proche de celle de l'*Arctica islandica* ainsi que de celle de Vénérides tels *Tivela stultorum*, et il est donc probable que *Calyptogena* est apparentée à ces espèces plutôt qu'à *Cardita*, comme DALL l'avait pensé.

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PLANCHE I

FIG. 1. (left above)

Calyptogena ponderosa Boss. (X 750) Tangential section of upper ectostratum. Margin of shell upwards. The " walls " partly enclosing the grains are clearly seen, as are the " luminous granules " within the grains.

FIG. 2. (right above)

Calyptogena ponderosa Boss. (X 50). Longitudinal section, showing lower ectostracum, mesostracum and upper endostracum. Shell margin to the right. 1, 2, 3 = lower quarter of ectostracum; 5 = mesostracum; 6 = endostracum. Light spots in ectostracum are mostly grains, in endostracum grain -or granular-sized luminous spots. In ectostracum, 2 represents the portion of the lower fraction of the layer at extinction, with dark " ground " and a few light grains; 3 is the coarse-grained sublayer just above the mesectostracal boundary. Although almost at extinction, the endostracum is lighter than the mesostracum and shows patches with luminous spots as well as the outlines of presumably complex major structures (vertical stripes).

FIG. 3. (below)

Calyptogena pacifica Dall (X 50). Longitudinal section through a valve, showing the relatively thick mesostracum (2-3) the thin grained ectostracum 1 and the endostracum 4. The myostracum consists of the broken oblique lines between 3 and 4, whose boundaries are indicated by XX. The strong line above this, between 2 and 3, whose ends are similarly labeled, is a growth line within the mesostracum.